

THE GENUS *CELAENEPHES* SCHMIDT-GÖBEL:
CHARACTERISTICS, SPECIES, AND RELATIONSHIPS
(COLEOPTERA: CARABIDAE: LEBIINI)

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Abstract.—Based on structural features of adults, the Indo-Australian *Celaenephes* Schmidt-Göbel (type-species: *C. parallelus* Schmidt-Göbel, 1846) is included in a monobasic subtribe, Celaenephina, postulated to be the most ancestral of the known extant subtribes of Lebiini. Apotypic features of the Celaenephina include: lateral areas of elytra and ventral surface of body with a sparse vestiture of short setae; front and middle trochanters and stylomere 2 of the ovipositor each with unusually long setae; ventral surfaces of antennomeres 4-11 each with an ovoid pit containing numerous sense organs; left mandible without a terebral tooth, but with an anterior retinacular tooth; maxillary galeomere 2 with setae apically; labium with paraglossae broad, broadly adnate to glossal sclerite, and anterior margins truncate; metathoracic wing with shortened oblongum cell; and abdominal tergum VIII and sternum X markedly sclerotized. Alternatively, interpretation as apotypic of the seemingly plesiotypic features of body color, tarsi, pronotal shape, ovipositor, and male genitalia, plus the apotypic feature of setation of the elytra and the front coxal cavities possibly secondarily uniperforate, form the basis for considering *Celaenephes* as a close relative of the subgenus *Cymindis* Latreille. In addition to the type species, *C. parallelus* (junior synonyms, *C. foersteri* Bouchard, 1903 and *Fukuchina sanadai* Habu, 1960; range, the Indian sub-continent eastward to northeastern Australia, and northward through the Philippine Islands and Taiwan to the Japanese Archipelago), the genus includes *C. linearis* (Walker) (junior synonyms, *Taromorpha alternata* Blackburn, 1894 and *C. rechingeri* Csiki, 1915; range, Sri Lanka and India eastward through Burma, Indo-China and the Indo-Australian Archipelago to Australia, New Caledonia, the Solomon Islands and Samoa, and northward through the Caroline and Philippine Islands to the Ryukyu Archipelago). Adults of the two species are distinguished from one another by differences in color of appendages, details of the elytral surface, and form of the apices of the elytra. Males are further distinguished by differences in form of the middle tibiae and in form of the median lobe.

During the last century, men of nous were familiar with the classic languages. Even so, it seems remarkable that H. M. Schmidt-Göbel (1846: 77) knew and published the ancient word from Homeric Greek, "*Celaenephes*," as a name for

a seemingly non-descript lebiine adult. The word means "shrouded in dark clouds." Schmidt-Göbel did not explain why he chose this name, though the dark cuticle of specimens of this genus probably provided the required inspiration.

Such a name might also have implied uncertainty about relationships of this genus. However, the author specified that it was probably related to *Arsinoe* Laporte, suggesting that he was not troubled by concern about relationships. The name, nonetheless, was prophetic. Relationships of the genus were, in fact, uncertain. Lacordaire (1854: 138) included it in the *Péricalides*, a taxon now ranked as a subtribe (*Pericalina*) of *Lebiini* (Ball, 1975). Bates (1886: 211) considered *Celaenephes* as a cymindine, related to *Dromius*. Csiki (1932: 1412), Jedlička (1963: 299), and Habu (1967: 250) included this genus in the subtribe *Dromiina*. Basilewsky (1984: 528) stated that *Celaenephes* was certainly not a lebiine but rather a platynine. He did not indicate to what group of platynines *Celaenephes* was related.

Specimens were sufficiently obscure and thus difficult to characterize that the genus escaped the attention of some subsequent workers. Thus, Blackburn (1894: 85) proposed the generic name *Taromorpha* for a specimen of *Celaenephes* collected in eastern Australia, and Habu (1960) proposed the name *Fukuchina* for material of *Celaenephes* collected in Japan.

Problems with recognition of the genus were paralleled by problems with recognition of species. Six specific epithets were proposed in the following combinations: *C. parallelus* Schmidt-Göbel; *Leistus linearis* Walker, 1858; *Taromorpha alternata* Blackburn, 1894; *C. foersteri* Bouchard, 1903; *C. rechingeri* Csiki, 1915; and *Fukuchina sanadai* Habu, 1960. Bates (1886: 211) remarked, when synonymizing the names *Celaenephes parallelus* and *Leistus linearis* Walker that: "the reference of a *Truncatipenne* allied to *Dromius* to the genus *Leistus* must be considered one of Walker's greatest feats of random identification." Possibly so, but the seeming dark clouds that enshrouded *Celaenephes* may have obscured Walker's vision.

Andrewes (1930a: 81) listed *L. linearis*, *T. alternata*, *C. foersteri*, and *C. rechingeri* as junior synonyms of *C. parallelus*, and Habu (1967: 250) added *F. sanadai*.

Thus, in 1967, *Celaenephes* was recognized as a monobasic genus, within the subtribe *Dromiina*. Habu (*loc. cit.*, p. 210), however, noted that the features of the ovipositors of *Celaenephes* females were not consonant with ovipositors of other *dromiines*. Based on this consideration, Habu (1982: 113–114) removed *Celaenephes* from the *Dromiina*, erecting a new monobasic subtribe, *Celaenephina*, to include it. Ball and Hilchie (1983: 112, 204) independently reached this conclusion. Habu (*loc. cit.*, pp. 113–114) indicated that he regarded the *celaenephine* ovipositor as derived, having evolved toward more complete development of the stylomeres. Ball and Hilchie (*loc. cit.*, pp. 113–114) stated that the ovipositor was primitive, overall.

Two of the present authors (D.S. and G.E.B.) decided to review more extensively the position of *Celaenephes*, and in the process of examining some borrowed material, discovered that the genus included two different forms rather than only the one (*C. parallelus* Schmidt-Göbel), as recognized recently. At this stage, advice and assistance were sought from R. B. Madge; his contributions, communicated

in letters and based on study of specimens in the collections at the British Museum (Natural History) and on examination of the literature, became sufficiently extensive to require including him as a third author. Together, we reviewed the evidence for recognition of the subtribe *Celaenephina*, and for the recognition of two species of *Celaenephes*, rather than one.

MATERIAL

This study was based on examination of 449 adult carabids representing the genus *Celaenephes*. As a basis for detailed comparison of character states of *Celaenephes*, 20 specimens of other taxa were dissected to verify published details, or to determine range of variation of particular features. These taxa were represented: *Calathus ingratus* Dejean, *Synuchus dubius* LeConte, and *Platynus decentis* Say (Tribe Platynini); *Peronoscelis latipennis* Chaudoir, and *Masoreus* species (Tribe Cyclosomini); and members of the tribe Lebiini—*Phloeoxena herculeano* Ball, and *Coptodera elongata* Chaudoir (subtribe Pericalina); *Apenes* species (subtribe Apenina); *Cymindis* (*Pinacodera*) *chevrolati* Dejean (subtribe Cymindina); *Euproctinus subdeletus* Bates (tentatively, subtribe Metallicina); *Agra* species (subtribe Agrina); *Gallerucidia erotyloides* Bates and *Calleida* species (subtribe Calleidina); *Dromius flohri* Bates (subtribe Dromiina); and *Lebia urania* Bates (subtribe Lebiina).

Specimens of *Celaenephes* were borrowed from the following institutions. Associated acronyms are used in the text to indicate source of particular specimens.

- BMHH Department of Entomology, Bernice P. Bishop Museum, 1355 Kalihi St., P.O. Box 19000-A, Honolulu, Hawaii 96819, U.S.A.
- BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD, England
- CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.
- RTB R. T. Bell Collection, Department of Zoology, The University of Vermont, Burlington, Vermont 05405, U.S.A.
- SMNH Section of Entomology, Swedish Museum of Natural History, S-104 05 Stockholm, Sweden
- USNM Department of Entomology, United States Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Type material was loaned to us by the Department of Entomology, National Museum in Prague, Czechoslovakia.

METHODS

Material used for detailed comparison was restricted to the Tribe Platynini, and to those lebiine subtribes with which *Celaenephes* had been associated: Pericalina, Cymindina, and Dromiina. We noted in passing characteristics of other subtribes (Apenina, Metallicina, Calleidina, Agrina, and Lebiina), but did not record information about them because such was not essential for our study.

Because of the nature of this study, no attempt was made to obtain all available

material of *Celaenephes*, nor to assess in detail intraspecific variation. Rather, we worked with material that was readily available which we judged in terms of experience with other taxa to be adequate for our purposes.

For comparison, we used few representatives of other taxa, choosing for study characters about whose range of variation something was known. We assessed variation of few characters, principally those used by previous authors in establishing higher taxa of Lebiini. We examined as well a few autapotypic traits of *Celaenephes*.

Taxonomic and phylogenetic principles, criteria used for ranking taxa, and general working methods were the same as those previously described (see Ball and Shpeley, 1983), and are not repeated here.

Genitalia and sclerites of ovipositors were preserved in glycerine, in microvials. Mouthparts and wings that were removed were glued on small cards. Microvials and cards were pinned beneath the specimens from which the sclerites had been removed.

For examination and illustration of some structures, a stereo-electron microscope, Cambridge Model S-150, was used. Specimens were cleaned using a sonicator, and were then gold-coated.

TERMS FOR STRUCTURES

In addition to words established by years of general usage, we have used several that have so far appeared principally in publications about carabids. Attention is drawn to them here, in the interest of clarity.

For micro-units of surface sculpture bounded by lines of microsculpture ("micro-lines"), we use "sculpticell" (Allen and Ball, 1980: 486); for elytral stria, "interneur" (Erwin, 1974: 3-5). For abdominal terga and sterna, Roman numerals are used, the first visible sternum being II, and the last one that is normally not retracted, VII.

Sclerites and setae of the ovipositor are named according to a system fully explained by Ball and Shpeley (1983: 746-749). Surfaces are named according to their orientation with the ovipositor fully extended, rather than retracted. The retracted condition is seen in most dead specimens, and is the way that the ovipositor is carried except when in use. Thus, the surface that is ventral in the retracted position is lateral with the ovipositor extended, and is named accordingly, with other surfaces named correspondingly.

Two structures not previously noted in carabids were found; they are as follows. On the ventral surfaces of antennomeres 4-11, pits were noted, each containing a number of structures that seem to be sensory (Fig. 12). These cavities are named "sensory pits." On the ventral surface of each mandible is a groove that houses numerous pores, each with a filament (Fig. 17). Because these filaments seem to be secretions, the grooves containing them are named "secretory grooves."

SUBTRIBE CELAENEPIIINA

Recognition.—Adults of this group have the following combination of putatively apotypic (derived) character states: elytron with apical fringe of microsetae; ventral surface with sparse vestiture of short setae; front and middle trochanters each with a long seta; antennomeres 4-11 ventrally each with pit containing sensory organs (Fig. 12); left mandible with an anterior retinacular tooth, without

terebreal tooth (Figs. 15A, B); each mandible ventrally with a secretory groove (Figs. 15B, 16B, 17A, B); galeomere 2 of maxilla with apical half setose (Fig. 13); labium with paraglossae adnate to glossal sclerite (Fig. 14); elytra with apices subtruncate; tergum VIII completely sclerotized, without membranous area medially (Fig. 7); (cf. Figs. 24–26); sternum X sclerotized (Fig. 10). Females have the nematoid setae as long or longer than stylomere 2 (Figs. 21A, C).

Included taxa.—This subtribe includes only the genus *Celaenephes* Schmidt-Göbel.

Relationships.—This subtribe is here suggested to be the most ancestral group of extant lebiines, and the sister group of the remaining subtribes. Details supporting this hypothesis are presented, following taxonomic treatment of the genus and species.

Geographical distribution.—The range of this Old World subtribe extends from Sri Lanka and India eastward in the Oriental Region through the Indo-Australian Archipelago to eastern Australia, New Caledonia, and the Samoan Archipelago. Northward, the range extends through the Philippine Archipelago and Taiwan to the southern part of the Japanese Archipelago (cf. Figs. 22 and 23).

Celaenephes Schmidt-Göbel

Celaenephes Schmidt-Göbel, 1846: 78–79. TYPE SPECIES: *Celaenephes parallelus* Schmidt-Göbel, 1846: 78 (by monotypy).—Lacordaire, 1854: 138.—Bates, 1892: 420.—Andrewes, 1927a: 272.—1927b: 11.—1930a: 81.—1930b: 337.—Csiki, 1932: 1412.—Jedlička, 1963: 299.—Habu, 1967: 249–250.—Darlington, 1968: 135.—Habu, 1982: 113–114.—Ball and Hilchie, 1983: 112 and 204.

Taromorpha Blackburn, 1894: 85. TYPE SPECIES: *Taromorpha alternata* Blackburn, 1894: 85 (by monotypy).—Andrewes, 1927a: 272.

Fukuchina Habu, 1960: 4–5. TYPE SPECIES: *Fukuchina sanadai* Habu, 1960: 5–6 (by monotypy).—Jedlička, 1963: 430–431.—Habu, 1967: 249.

Notes about synonymy.—Andrewes (1927a: 272) synonymized the names *Taromorpha* and *Celaenephes* without presenting supporting statements. We have seen type material of both type species and believe that they are congeneric.

Habu (1967: 249) synonymized the names *Fukuchina* and *Celaenephes*. We have not seen the holotype of *F. sanadai* Habu, but illustrations of type material (*loc. cit.*, figs. 421–428) show that Habu (1960) had in hand specimens of *C. parallelus* on which he based the description of the type species of *Fukuchina*.

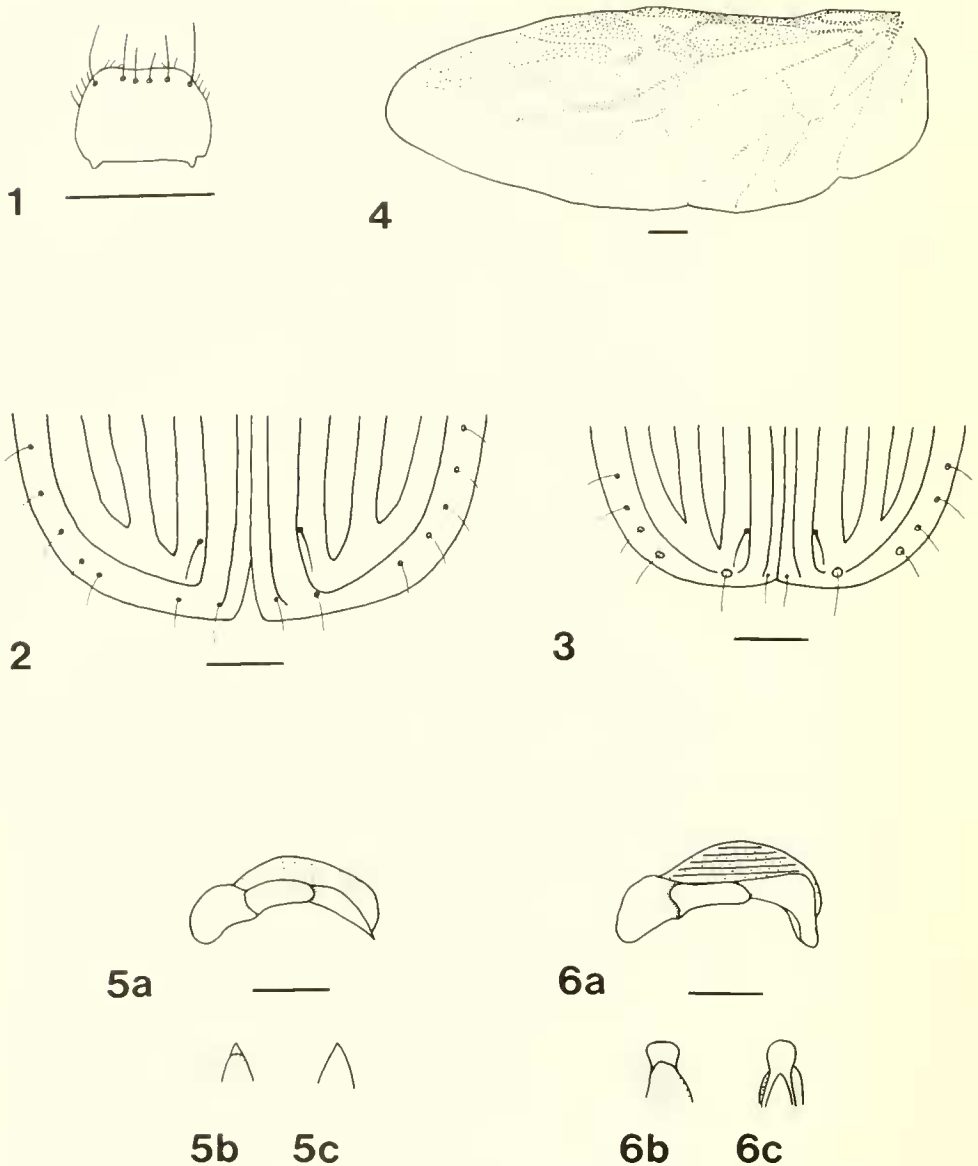
Description.—Standardized Body Length 5.32–7.36 mm (males) and 5.60–7.16 mm (females).

Color.—Head, thorax, and abdominal sterna castaneous to black, antennae and mouthparts testaceous to black.

Microsculpture.—Dorsal surface with mesh pattern isodiametric, microlines faint on clypeus, frons, vertex, and disc of pronotum; more easily seen laterally on pronotum and elytra. Ventral surface with mesh pattern slightly transverse on head near eyes, thoracic sterna, pterothoracic pleura, and abdominal sterna medially; isodiametric on proepisternum and abdominal sterna laterally; microlines not evident medially on head.

Luster.—Surface moderately shining.

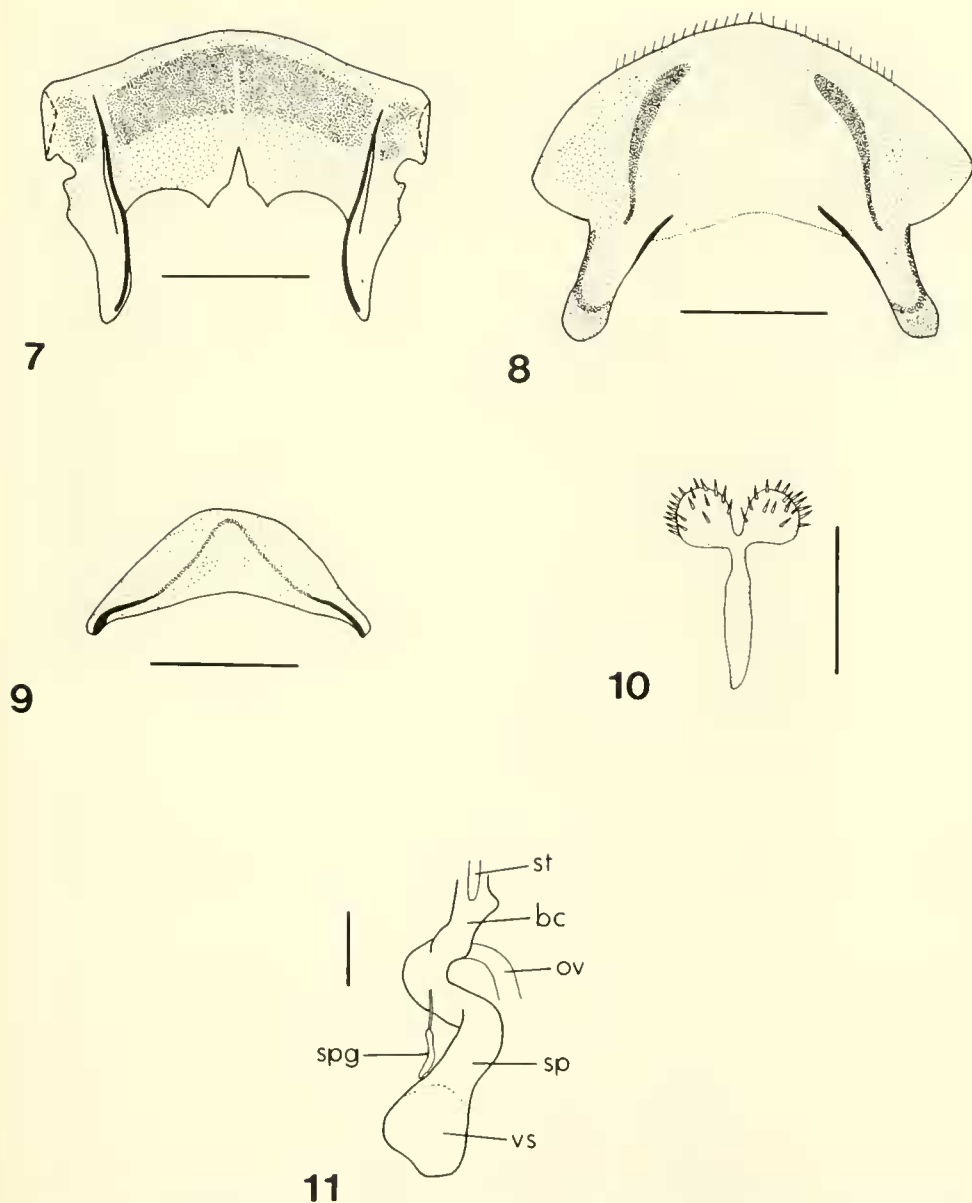
Fixed setae.—Typical for Lebiini, those of fore and middle trochanters longer than normal.



Figs. 1-6. Line drawings of sclerites of *Celaenephes* adults (scale bars = 0.50 mm). 1, labrum of *C. linearis*. 2-3, Apices of elytra: 2, *C. parallelus*; 3, *C. linearis*. 4, Left hind wing of *C. linearis*. 5-6, Male genitalia (A, median lobe and left paramere, left lateral aspect; B and C, median lobe, dorsal and ventral aspects, respectively). 5, *C. parallelus*. 6, *C. linearis*.

Vestiture.—Elytra with intervals 7, 8, and 9 with sparse covering of fine short setae. Ventral surface of head with few fine setae near eyes. Palpomeres, thoracic and abdominal sterna and metepisterna finely setose. Fore coxae with few short setae. Middle coxae with numerous moderately long and few markedly longer setae. Hind coxae with lateral-posterior margins fringed with numerous long setae. Tarsomeres with dorsal surfaces setose.

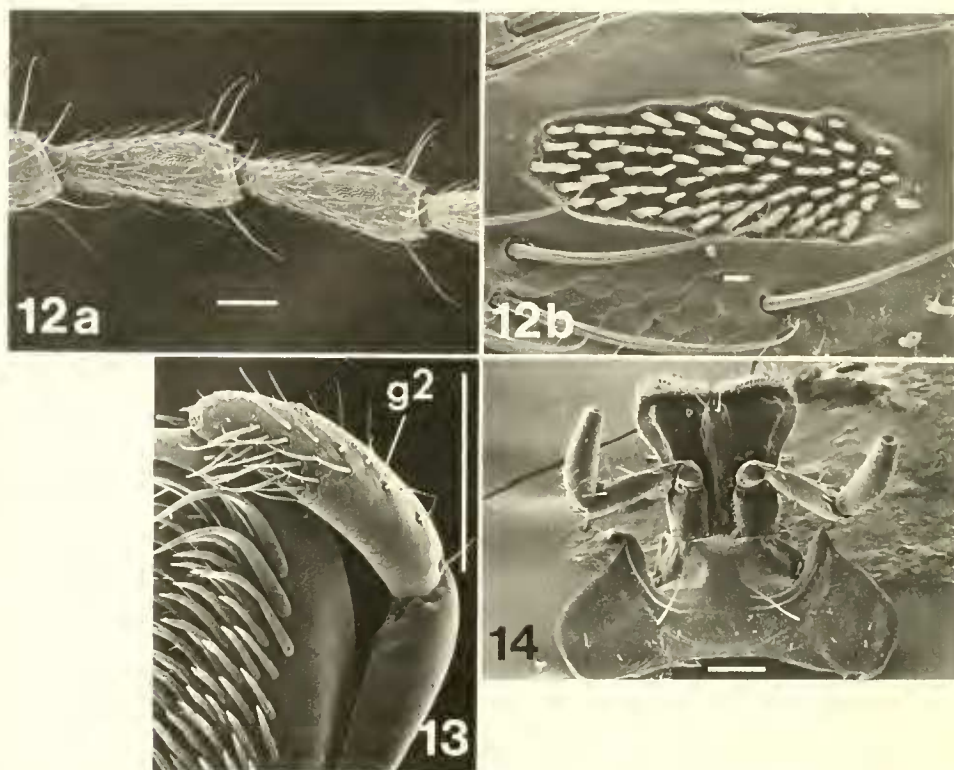
Head.—Labrum as in Fig. 1. Frons smooth with fine punctures. Clypeus rect-



Figs. 7-11. Line drawings of structures of *Celaenephes linearis* adults (scale bars = 0.50 mm). Figs. 7-10, terminal abdominal sclerites. 7, Tergum VIII. 8, Sternum VIII. 9, tergum X. 10, Sternum X. 11, Female reproductive tract and associated sternum X, dorsal aspect. (bc, bursa copulatrix; ov, oviduct; sp, spermatheca; spg, spermathecal gland; st, sternum X; vs, ventral sclerite).

angular, with anterior margin straight. Eyes large, subgenae very small. Antennae of average length, extended beyond base of pronotum. Antennomeres 2 and 3 each with ring of setae apically, few fine setae scattered over surface. Antennomere 4 setose in apical three fourths; antennomeres 5-11 generally setose. Antennomeres 4-11 each with ventral sensory pit (Figs. 12A, B).

Mouthparts.—Left mandible (Figs. 15A, B) with cutting edge formed by retinac-

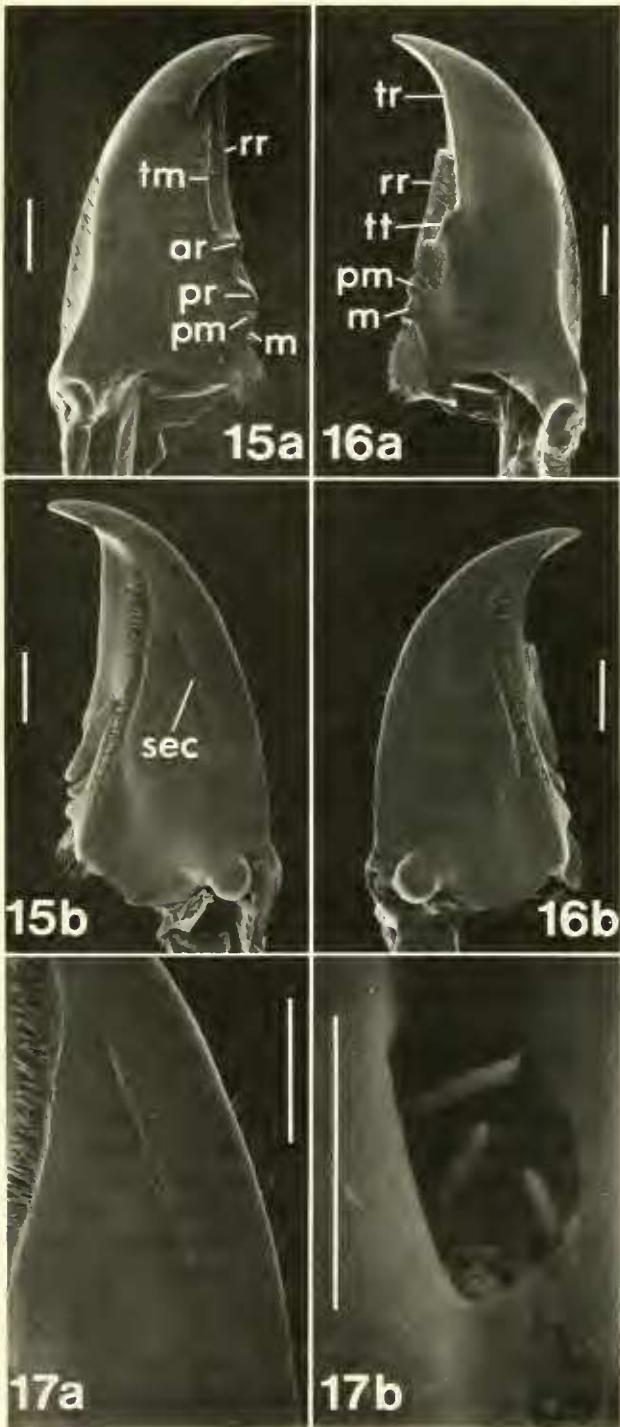


Figs. 12–14. SEM photographs of sclerites of *Celaenephes* adults. 12, Antenna, ventral aspect, of *C. linearis*. (A, antennomeres 7–10 (scale bar = 100 μ m); B, antennomere 9, enlargement to show detail of sensory pit (scale bar = 5 μ m). 13–14, Mouthparts of *C. linearis*. 13, Left maxilla, ventral aspect (scale bar = 100 μ m), g2, galeomere 2. 14, labium ventral aspect (scale bar = 100 μ m).

ular ridge; posterior retinacular tooth prominent; anterior retinacular, premolar, and molar teeth present. Right mandible (Figs. 16A, B) with cutting edge formed by terebral ridge; terebral, retinacular, premolar and molar teeth present. Both mandibles ventrally with long secretory groove (Figs. 17A, B). Maxillae average for *Lebiini*; galeomere 2 setose near apex (Fig. 13); maxillary palpomere 4 fusiform, subequal in length to palpomere 3. Labium with ligula (Fig. 14) with large membranous paraglossae, densely setose along lateral margins, broadly adnate to glossal sclerite; latter narrow, with two long setae apically; labial palpomere 3 fusiform, subequal in length to bisetose palpomere 2; mentum edentate.

Thorax.—Pronotum slightly convex, wider than long; anterior margin slightly concave, posterior margin slightly convex; anterior angles rounded, posterior angles obtuse; lateral margins reflexed; side sinuate before posterior angles. Pro-

Figs. 15–17. SEM photographs of mandibles of *C. linearis* adults. 15A and B, left mandible, dorsal and ventral aspects, respectively. 16A and B, Right mandible, dorsal and ventral aspects, respectively (scale bars = 100 μ m) (ar, anterior retinacular tooth; m, molar; pm, premolar tooth; pr, posterior



retinacular tooth; rr, retinacular ridge; sec, secretory groove; tm, terebral margin; tr, terebral ridge; tt, terebral tooth). 17A, Portion of left mandible, ventral aspect, showing secretory groove (scale bar = 100 μ m); 17B, enlargement of 17A, showing detail of secretory groove (scale bar = 2 μ m).

sternum with intercoxal process bisetose. Anterior coxal cavities uniperforate. Pterothorax with metepisternum elongate, lateral margin about twice as long as anterior margin.

Elytra.—Widened apically; apical angle either obtuse and preapical angle slightly rounded (Fig. 2), or apical angle nearly rectangular, and preapical angle markedly rounded (Fig. 3). Interneurs shallow; intervals broad, only slightly convex. Interval 3 with three setigerous punctures. Interval 4 uniformly convex, or depressed medially. Umbilical series with 22 or fewer (average 20) setigerous punctures. Basal ridge incomplete (Fig. 18A), extended only to near base of interneur 4; apex with fringe of fine setae (Fig. 18B).

Hind wings.—Fully developed, oblongum cell reduced, wedge cell present (Fig. 4).

Legs.—Long and slender, hind tarsus and tibia subequal (length hind tarsus/length hind tibia = 0.85) in length. Middle tibia of male either unmodified (Fig. 20), or with notch in ventral surface (Fig. 19). Males with tarsomeres 1–3 of front leg with adhesive vestiture biseriate. Tarsal claws smooth, not pectinate.

Abdomen.—Sterna IV, V, and VI each with one pair of long (ambulatory) setae. Sternum VII of male with one pair of anal setae, female with two pair. Tergum VIII (Fig. 7) sclerotized throughout; sternum VIII (Fig. 8) membranous medially. Tergum X as in Fig. 9; sternum X (Fig. 10) well developed.

Male genitalia.—Median lobe slender, dorsal surface to basal bulb membranous, membrane either smooth (Fig. 5A) or carinate; apex in ventral aspect slender and pointed (Figs. 5B, C), or thickened and broadly rounded (Figs. 6B, C); apical orifice dorsal. Internal sac without armature. Parameres subequal in length, apices of each broadly rounded.

Ovipositor.—Stylomere 1 setose medially near apex (Fig. 21A). Stylomere 2 (Figs. 21A, B) falcate, with broadly rounded apex; one dorsal ensiform seta medially, two to four laterally; nematoid setae as long or longer than stylomere 2.

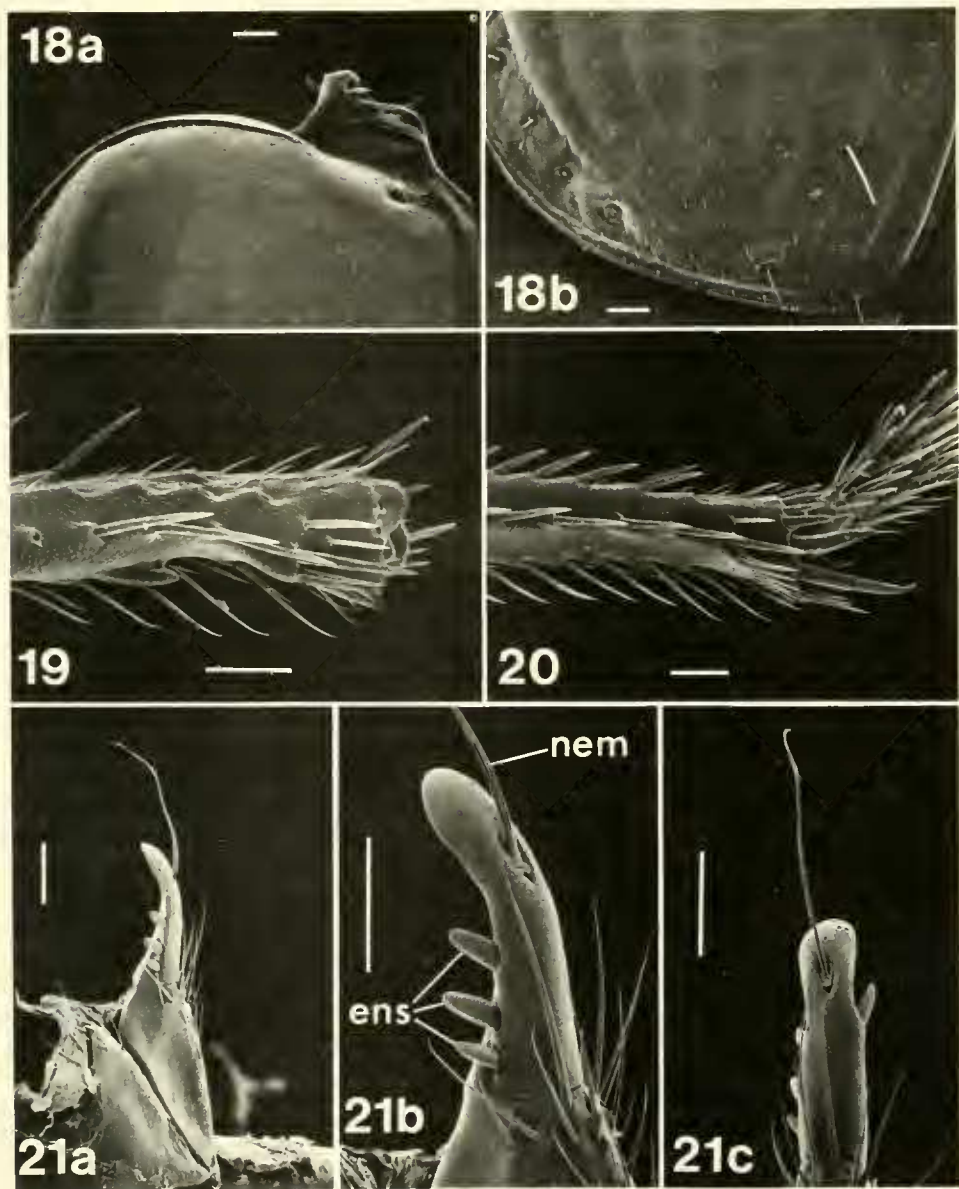
Female genitalia.—*Bursa copulatrix* reduced; spermatheca very large, with terminal sclerite ventrally; spermathecal gland present (Fig. 11).

KEY TO SPECIES OF *CELAENEPHES* SCHMIDT-GÖBEL, BASED ON FEATURES OF ADULTS

1. Terminal palpomeres with only apices pale, latter markedly contrasted with dark bases. Elytron with interval four even, surface not depressed at middle. Middle tibia of male with inner (i.e., ventral) margin with single deep notch, preapically (Fig. 19), and median lobe of genitalia with apex pointed (Figs. 5B, C) *C. parallelus* Schmidt-Göbel.
- Terminal palpomeres pale, almost without contrast between base and apex. Elytral interval 4 of most specimens with shallow depression at middle. Male with inner margin of middle tibia with series of shallow emarginations (Fig. 20), and median lobe of genitalia with apex broad (Figs. 6B, C) *C. linearis* (Walker).

Celaenephes parallelus Schmidt-Göbel

Celaenephes parallelus Schmidt-Göbel 1846: 78–79. TYPE MATERIAL: one male and three females. LECTOTYPE (here selected), male, labelled: MUS. PRAGENSE TENASSERIM COLL. HELFER; Typus! teste Dr. J. Obenberger



Figs. 18–21. SEM photographs of sclerites of *Celaenephes* adults (scale bars = 100 μ m). 18, Left elytron, dorsal aspect, of *C. linearis*. (A, base; B, apex). 19–20, Middle tibiae, anterior aspect, apical portion. 19, *C. parallelus*. 20, *C. linearis*. 21, Left stylomeres 1 and 2 of ovipositor of *C. linearis*. (A, stylomeres 1 and 2, lateral aspect; B and C, stylomere 2, lateral and ventral aspects, respectively; ens, ensiform setae; nem, nematoid setae (scale bars = 100 μ m)).

[red paper]; parallelus Sch. G. COL. HELFER [handwritten above type]; Mus. Nat. Pragae Inv. 26638 [orange paper]; PARALECTOTYPES: two females, Nos. 26636 and 26637 labelled as above. One female labelled: MUS. PRAGENSE COLL. HELFER; Burma Helfer [handwritten]; Typus! teste Dr. J.

Obenberger [red paper]; *parallelus* Sch. G. COL. HELFER [handwritten above type]; Mus. Nat. Pragae Inv. 26635 [orange paper] (National Museum in Prague, Czechoslovakia). TYPE LOCALITY: Burma, Tenasserim.—Bates, 1886: 211.—1892: 420.—Andrewes, 1919: 188.—1923: 46.—1927a: 272.—1927b: 11.—1929: 314.—1930a: 81.—1930b: 337.—1947: 12.—Csiki, 1932: 1412.—Landin, 1955: 405, 466.—Jedlička, 1963: 399–400.—Habu, 1967: 250–253.—Darlington, 1968: 135.

Celoenephes (sic) parallelus; Bouchard, 1903: 176.—Habu, 1967: 251.

Coloenephes (sic) foersteri Bouchard, 1903: 176. TYPE MATERIAL: Not seen. TYPE AREA: Sumatra.—Andrewes, 1927b: 11.—1930a: 81.

Fukuchina sanadai Habu, 1960: 5–6. TYPE MATERIAL: not seen. HOLOTYPE female, labelled: VIII.7, 1956 Mt. Fukuchi K. Sanada leg. TYPE LOCALITY: Fukuoka Prefecture, North Kyushu, Japan.—Jedlička, 1963: 430–431.—Habu, 1967: 251.

Celaenephes parallelus (in part); Darlington, 1968: 135.

Notes about synonymy.—Andrewes (1930a: 81) synonymized the names *C. parallelus* and *C. foersteri*. We have not seen type material of the latter named form, but accept the synonymy, reasoning as follows. Bouchard compared the character states of *C. foersteri* with those of *C. parallelus*, and from the statements made, we believe that Bouchard identified specimens of *C. linearis* (Walker) as *C. parallelus*. Thus, Bouchard's new species was the true *C. parallelus*, the specimens in question being smaller and darker. Habu (1967: 250) synonymized the names *F. sanadai* and *C. parallelus*. For further details, see synonymical notes under the genus *Celaenephes*.

Recognition.—In addition to features presented in the key, adults have piceous to black antennae and mouthparts, and the sutural angle of the elytron is rounded (Fig. 2). Standardized Body Length ranges as follows: 5.32–6.04 mm (males) and 5.60–6.60 mm (females).

Notes about habitat and life history.—Adults of this species are probably arboreal, as are those of *C. linearis*. However, only one specimen (from New Guinea) that we have seen is associated with habitat data: "on maize leaf." Because maize is an introduced species of plant, the association of it and *C. parallelus* may be evidence that the latter species can survive in habitats disturbed by man.

Collecting records extend from May to November, and specimens have been collected at light from May to September. Adults may be active fliers throughout the year, but this cannot be established from the few available records.

Remarks about *C. parallelus* by Darlington (1968: 135) refer principally to *C. linearis*.

Geographical distribution (Fig. 22).—The range of this species extends from India (Amalai Hills, Madras [B. P. Moore, personal communication]) to north-eastern Australia, and through the Philippines and Taiwan to Kyushu Island in the Japanese Archipelago. (The Australian specimens [male and three females] were collected at Cardstone, North Queensland, November 15–28, 1966 [B. P. Moore, CSIRO, personal communication]). The seemingly isolated occurrences of *C. parallelus* in New Guinea and Australia are likely to be artifacts of collecting, rather than representing populations far removed from the other populations of the species.

Chorological affinities.—The ranges of *C. parallelus* and *C. linearis* overlap

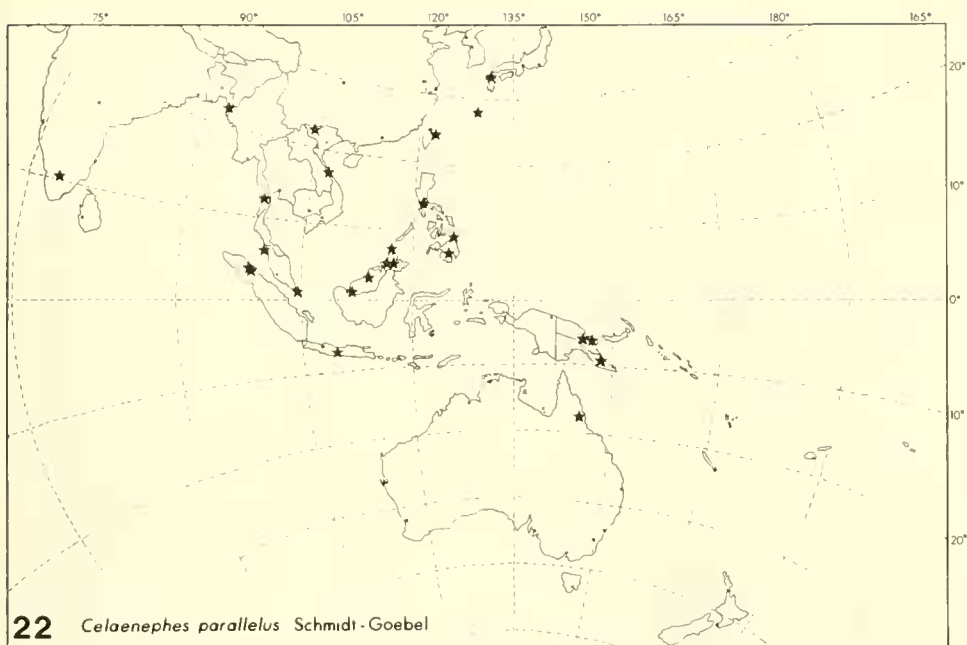


Fig. 22. Geographical distribution of *Celaenephes parallelus*.

broadly (cf. Figs. 22 and 23). Furthermore, both species have been taken at the same localities in Burma, Viet Nam, the Philippine Islands, Sabah, Sarawak, the Riouw Archipelago off Sumatra, New Guinea, and Australia. Such extensive sympatry, both general and specific, provides good presumptive evidence that the two forms, established on morphological differences, are indeed reproductively isolated from one another, and hence are specifically distinct. However, the extensive overlap prevents inferring the location or nature of the barrier that led to the differentiation of the ancestral stocks of the two species. It remains to be determined if they occupy different habitats, and the role of structural differences in maintaining their reproductive isolation.

Material examined.—We have seen 42 specimens including types of this species. Non-type material was seen from the following localities: BANGLADESH. Sitapahar R., Chittagong, H.T. (BMNH). BURMA. Myitkyina, 175 m (SMNH). Tenasserim (BMNH). INDONESIA Java. Djeroeklegi, Zuid-Banjoemas (BMNH). Sumatra. Riouw Arch. (BMNH). Sumatra's O.K., Soengei Merah (BMNH). Tijinta Radja (BMNH). MALAYSIA Sabah-Borneo. Borneo North (BMNH). 5 mi S Mt. Trus Madi, 1800 ft (BMNH). R. Karamuak, 7 mi SSE Telupid (BMNH). Tawai Plat., 8 mi S Telupid, 1300 ft. (BMNH). Sarawak-Borneo. foot of Mt. Dulit, jct. of rivers Tinjar & Lejok (BMNH). LUBOK ANTU (BMNH). Malaya. Penang. (BMNH). PAPUA. New Guinea. Goroka, 1550 m (MCZ). Madang Dist., Finisterre Mts., 3500 ft (BMNH). Oro Bay (MCZ). Popondetta (MCZ). Wabag (RTB). Wau (RTB). PHILIPPINE ISLANDS. Balabac (BMNH). Mindanao I.: (BMNH); Davao (BMNH) (USNM); Surigao (BMNH) (USNM). Luzon I., Laguna, Mt. Makiling (CAS). VIET NAM. Quang Tri Prov.: 1 mi N Quang Tri (USNM); Cam Lo, 7 mi W Dong Ha (USNM). Tonkin, Chapa (BMNH).

Celaenephes linearis (Walker)

Leistus (?) *linearis* Walker, 1858: 203. HOLOTYPE male, labelled: Type, H. T. [white disc, ringed with red]; Ceylon [handwritten, on pale blue disc], 59 106 [on under surface]; *Leistus*? *linearis* Walker Ann. N. Hist. (Type) [handwritten, on blue paper] (BMNH). TYPE AREA: Ceylon.—Bates, 1886: 211.—Andrewes, 1919: 188.—1927b: 11.—1930a: 81.—Csiki, 1932: 1412.—Habu, 1967: 250.

Taromorpha alternata Blackburn, 1894: 85. HOLOTYPE male, labelled: 4997 Cairns [handwritten in red ink on card supporting specimen]; Type [white disc, ringed with red]; Australia, Blackburn Coll., B.M. 1910-236; *Taromorpha alternata*, Blackb. [handwritten]. (BMNH). TYPE LOCALITY: Cairns, Australia. NEW SYNONYMY.—Andrewes, 1927a: 272.—1927b: 11.—1930a: 81.—Csiki, 1932: 1412.—Jedlička, 1963: 399.—Habu, 1967: 250.

Celaenephes rechingeri Csiki, 1915: 164. LECTOTYPE (here selected) teneral male, labelled: Upolu Samoa Rechinger; *Celaenephes Rechingeri* m. Typus! [in red ink] det. Csiki [handwritten]; borrowed fr. Budapest Mus. (MCZ). PARALECTOTYPE female, labelled: Savaii Samoa Rechinger '05; *Celaenephes Rechingeri* m. Typus! [in red ink]; det. Csiki [handwritten]; borrowed fr. Budapest Mus. (MCZ). PARALECTOTYPES (sex not determined), labelled as above, one from Savaii, two from Upolu (Naturhistorisches Museum Wien).—TYPE LOCALITY: Samoa, Upolu Island. NEW SYNONYMY.—Andrewes, 1927b: 11.—1930a: 81.—Csiki, 1932: 1412.—Jedlička, 1963: 399.—Habu, 1967: 251.

Celaenephes parallelus (in part); Habu, 1967: 251.—Darlington, 1968: 135.—1970: 43.

Notes about synonymy.—Bates (1886: 211) synonymized *Leistus linearis* Walker with *C. parallelus* Schmidt-Goebel. This action was incorrect, for the holotype of *L. linearis* is clearly specifically distinct from the type of *C. parallelus*.

We have examined the types of *T. alternata* Blackburn, and *C. rechingeri* Csiki, and both are conspecific with the holotype of *L. linearis*.

Jedlička (1963: 399) records the location of the type of *C. rechingeri* as the Berlin Museum. However, we have seen specimens labelled as "type" in the Naturhistorisches Museum Wien, and in the MCZ; evidently Csiki labelled all of the specimens that he saw as "type." Thus, a lectotype designation is required, and we have provided one.

Recognition.—In addition to features presented in the key, adults have testaceous to castaneous antennomeres and mouthparts and the sutural angle of the elytron is nearly rectangular (Fig. 3). Standardized Body Length ranges as follows: 6.00–7.36 mm (males) and 5.92–7.16 mm (females).

Notes about habitat and life history.—Specimens of this species have been taken in a variety of habitats, as indicated by data on locality labels: in bases of bromeliad leaves (*sic*); beating trees; moss forest; undergrowth, secondary forest; and near fermenting tapioca.

Specimens have been collected throughout the year, but only from June to September north of the equator, and July to October south of the equator, at white or ultra-violet light. We have seen teneral specimens which were collected in June, July, and August in New Guinea, and in October and November in Australia.

Darlington (1968: 135) suggested that adults of *Celaenephes* may have reached

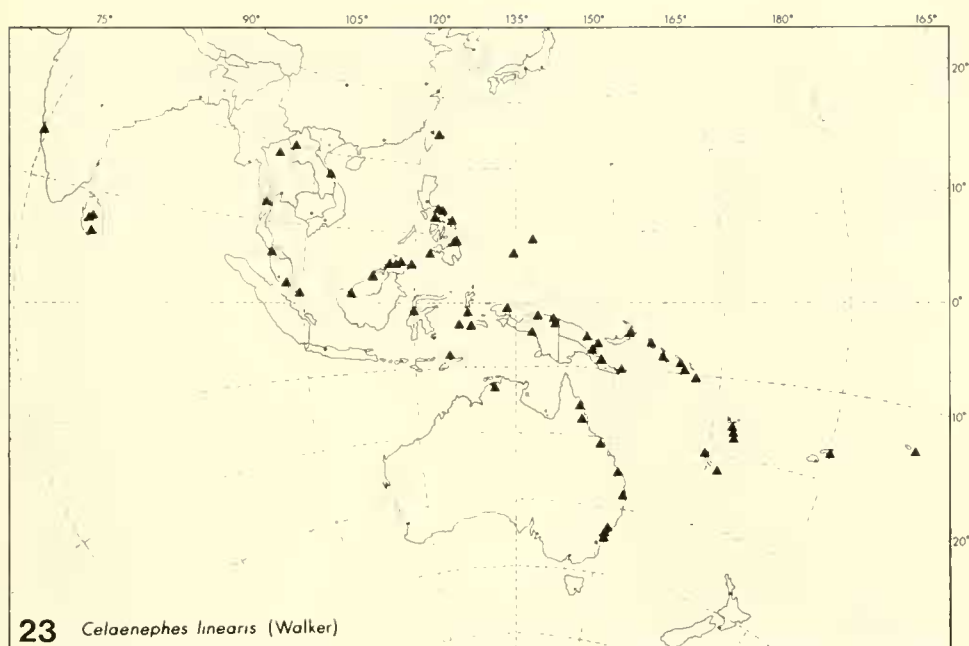


Fig. 23. Geographical distribution of *Celaenephes linearis*.

the Pacific islands by transportation in thatching material, this being a consequence of an arboreal way of life. Not recognizing that two species were included in the genus, he referred to *C. parallelus* only, though it is *C. linearis* that ranges into the Pacific Islands.

Geographical distribution.—The range of this species extends from Sri Lanka and India (Shimoga, Agumbe Ghat [B. P. Moore, CSIRO, personal communication]) in the Oriental Region eastward throughout the Indo-Australian Archipelago to the Samoan islands of Upolu and Savaii; southward to the northern and eastern coasts of Australia (including Cardstone, N. Queensland [B. P. Moore, CSIRO, personal communication]), and to New Caledonia. Northward, the range of *C. linearis* extends to Iriomote, the southernmost island of the Ryukyu Archipelago. The last-named record is based on fig. 425 (Habu, 1967: 252), which illustrates the apical portion of an elytron. Although Habu identifies the specimen as *C. parallelus*, the form of the elytron is characteristic of *C. linearis*. This species is also known from the Western Caroline Islands, the records being under the name *C. parallelus* (Darlington, 1970: 43).

Chorological affinities.—See this topic under *C. parallelus*.

Material examined.—We have seen 388 specimens including types. Non-type material was seen from the following localities: AUSTRALIA. New South Wales: Illawarra (BMNH); Newport, N. Sydney (BMNH); Ryde, W. Sydney (BMNH). Northern Terr., Stuart Hwy., Coomalie Ck. (CAS). Queensland: Cedar Ck. Falls, Tamorine (CAS); Eubenangee (BMNH); 8 mi NE Eungella, 950 m (CAS); 17 mi W Monto, 500 m (CAS). BURMA. Tenasserim (BMNH). FIJI ISLANDS. Taveuni (BMNH). Waiganitu (MCZ). INDONESIA Celebes. (BMNH). Lesser Sundas.

Poera, Ins. Allor, 3000–4000 ft. (BMNH). Moluccas. Amboina (BMNH). Buru (BMNH). Laiwui (BMNH). Sumatra. Riouw Arch. (BMNH). West Irian-New Guinea. Bodem, Saroni area (MCZ). Cyclops Mts., Sabron, 930 & 1200 ft. (BMNH) (MCZ). Hollandia (BMNH) (MCZ). Launch Camp, Setakwa Utakwa Exped. (BMNH); Maffin Bay (BMNH) (MCZ). Maffin Bay, Mt. Leamington, 1300–1500 m (MCZ). Njau-limon, S of Mt. Bougainville, 300 ft. (BMNH). Santani (MCZ). Vogelkop, Kebar Valley, w Manokwari, 550 m (MCZ). Waris, 450–500 m (MCZ). MALAYSIA Malaya. Casteln (BMNH). Malacca (BMNH). Talan Lintok, N. Kedah (BMNH). Sabah-Borneo. Borneo North (BMNH). R. Karamauk, 7 mi SSE Telupid, 200 ft (BMNH). Sandakan (BMNH)(USNM). Sook., 17 mi SE Keningau, 1500 ft. (BMNH). Tawai Plat., 8 mi S Telupid, 1300 ft. (BMNH). Sarawak-Borneo. (BMNH). DRTU's ROAD (BMNH). Kuching (BMNH). Mt. Dulit (BMNH). foot of Mt. Dulit, jct. of rivers Tinjar & Lejok (BMNH). Mt. Matang., 500–1000 ft. (BMNH). NEW CALEDONIA. (BMNH). Bouloupari, Oenghklou R. (MCZ). Plaine des lacs (BMNH). Pueblo coast, 1500 ft. (BMNH). Tinchialit, 2020 ft. (BMNH). PAPUA Bougainville Island. Piva River (MCZ). New Britain Island. Gazelle Peninsula, Upper Warangoi, 220 m. (MCZ); Matupi (MCZ). New Guinea. Bini-gusi, Gwariu R., 150 m (MCZ). Cape Killerton (MCZ). Dobadura (MCZ). Erima, Astrolabe Bay (MCZ). Finschafen (CAS)(MCZ). Ishurava, 3000 ft. (BMNH). Kokoda, 1200 ft. (BMNH). Morobe District: Kunai Creek (MCZ); Surprise Creek (MCZ); Wau (MCZ)(RTB); forestry road north of Wau (CAS). Wabag (RTB). Noramanby Island, Waikuna, Sewa Bay (MCZ). Popondetta (MCZ). PHILIPPINE ISLANDS. Basilan I. (BMNH)(USNM). Island Samar (USNM). Island Sibuyan (BMNH)(USNM). Luzon I.: Calabangan (CAS); Malinao, Tayabas (BMNH). Mindanao I.: Kabasalan, Zamboanga (CAS); Surigao (BMNH)(MCZ)(USNM). Sanga Sanga, Moorjawa (BMNH). SAMOA. Upolu, Apia (BMNH). SOLOMON ISLANDS. Guadalcanal I.: (MCZ); Honiara (BMNH)(CAS); Matanikau River (MCZ); Tapenanje, 1100 ft. (BMNH); Tenaru River (MCZ). Kolombangara I., Ringi Cove, 23–24 km up main road (CAS). San Cristobal Island, Wainoni (BMNH). San Jorge (BMNH). SRI LANKA. Balangoda (BMNH). Gal District, Udugama Kanneliya Jungle, 240 m. (USNM). Mon. District, Monaragala (USNM). Pol District, Sigirya (USNM). THAILAND. E slope, Doi Sutep, 260 m (CAS). VANUATU (= New Hebrides). Aneityum (BMNH). Malekula I. (BMNH). Tanna (BMNH). VIET NAM. Quang Tri Prov., Cam Lo, 7 mi W Dong Ha (USNM). WESTERN CAROLINE ISLANDS. Palau-Babelthaup (BMNH). Yap (BMNH). COUNTRY NOT DETERMINED: Borneo. (BMNH)(USNM). New Guinea—country not found. Fenichel (MCZ). Lao (MCZ).

RELATIONSHIPS OF *CELAENEPHES* SCHMIDT-GÖBEL

The authors have not been able to achieve consensus about the relationships of *Celaenephes*. Two of us (D.S. and G.E.B.) believe that *Celaenephes* is not closely related to other extant genera of lebiines. One of us (R.B.M.) believes that this genus is related to *Cymindis* (*sensu stricto*) Latreille. Because of the nature of a hierarchical system of classification, such differences of opinion are not easily accommodated: the former hypothesis leads to placing *Celaenephes* in a monobasic subtribe, as Habu (1982) has done. The latter hypothesis, in a phylogenetic system of classification, requires inclusion of *Celaenephes* in the subtribe *Cymindina*. Evidence for each hypothesis follows, though the hypothesis favored by Shpeley and Ball prevails in formally classifying *Celaenephes*.

CELAENEPHES AND THE SUBTRIBE CELAENEPHINA

Elements of the defining combination of character states of the subtribe Celaenephina are assessed below in terms of those states of lebiine subtribes in which the genus *Celaenephes* has previously been included (Pericalina, Cymindina, and Dromiina), using as an out-group the tribe Platynini. Choice of platynines as out-group is based on their generally more plesiotypic structures and on the likelihood of a close phylogenetic relationship between Platynini and Lebiini (Liebherr, 1983).

CHARACTERS AND CHARACTER STATES

Eighteen characters, diagnostic for lebiine subtribes, are used in assessing relationships. States of these characters are classified phylogenetically, and taxa are compared in terms of synapotypic states. The sequence of characters in the presentation is that in which their apotypic states would appear in a reconstructed phylogeny of the Lebiini.

The basis of classification of each state as plesiotypic (ancestral) or apotypic (derived) is out-group comparison, as explained by Wiley (1981: 139–146) and Watrous and Wheeler (1981).

01. Abdominal tergum VIII, lateral margin.—Two states: plesiotypic, lateral margins rounded, not produced as lobes (Fig. 24); apotypic, lateral margins produced as lobes (Figs. 7, 25, and 26). Each lobe is associated with the opening of a duct of the paired pygidial defense glands.

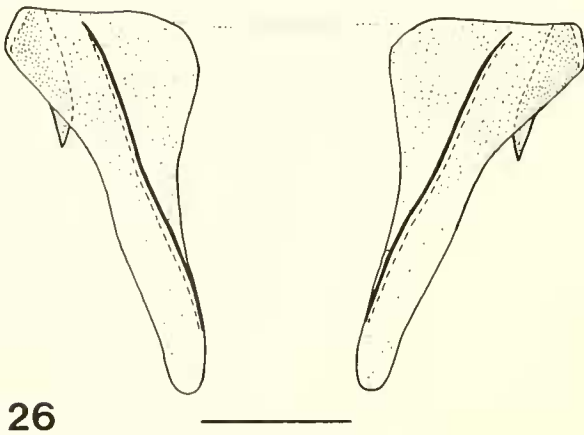
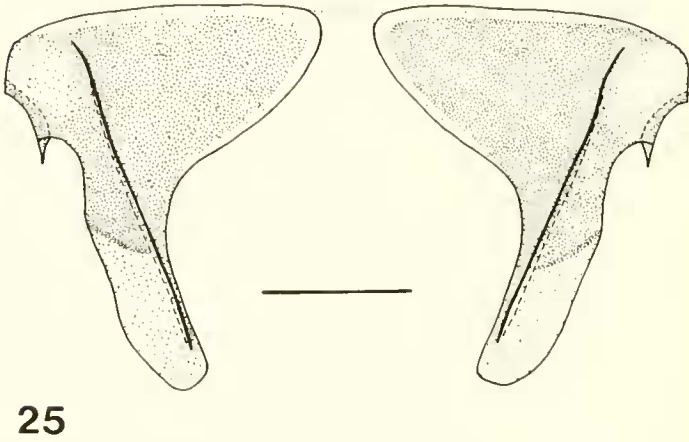
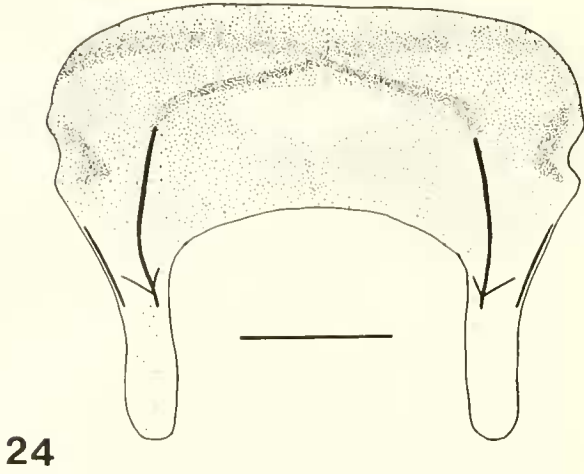
02. Mandibles, secretory groove.—Three states: plesiotypic, absent; two apotypic states—a, well developed, almost as long as terebra (Figs. 15B, 16B, and 17A, B); b, much shorter (*cf.* Ball and Hilchie, 1983: 140, figs. 41C, D, and 43C, D). Such grooves are widely distributed among lebiine genera, though in many, the grooves are lacking. We interpret this as a loss, based on phylogenetic analysis using celaenephines and pericalines as functional out-groups (Watrous and Wheeler, 1981) in relation to the generally more derived cymindines and dromiines.

03. Antennomeres 4–11, sensory pits.—Two states: plesiotypic, absent; apotypic, present (Figs. 12A, B). These pits and their associated sense organs are known among carabids only in adult lebiines of *Celaenephes* and of the seemingly unrelated genera *Euproctinus* Leng and Mutchler, and *Parena* Motschulsky (both genera tentatively assigned to subtribe Metallicina [see Basilewsky, 1984: 542–543, for a diagnosis of the group]).

04. Left mandible, anterior retinacular tooth.—Two states: plesiotypic, absent; apotypic, present (Figs. 15A, B).

05. Abdominal sternum X, extent of sclerotization.—Two states: plesiotypic, principally membranous; apotypic, principally sclerotized (Fig. 10). Although sternum X was no doubt sclerotized in ancestral carabids, this sclerotization is reduced in the more derived groups, including platynines. The condition in *Celaenephes* is interpreted as a reversal to a seeming plesiotypic condition. However, the sclerotization is in the form of a spicule rather than more or less rectangular, as a plesiotypic sclerite would have been (*i.e.*, the ventral counter-part of the rectangular tergum X, Fig. 9).

06. Left mandible, terebral tooth.—Two states: plesiotypic, present; apotypic, absent (Figs. 15A, B). Although the Pericalina and Dromiina are classified as plesiotypic for this character, this is only because at least some members of each of these subtribes exhibit a terebral tooth. The tooth is lacking from many mem-



Figs. 24–26. Line drawings of tergum VIII of selected platynine and lebiine females. 24, *Platynus decentis* Say. 25, *Cymindis chevrolati* Dejean. 26, *Lebia urania* Bates. (Scale bars = 0.50 mm.)

bers of these groups, and the absence is interpreted as a loss following origin of each subtribe.

07. Elytron, apical microsetae.—Two states: plesiotypic, absent; apotypic, present.

08. Elytron, form of apex.—Two states: plesiotypic, tapered preapically, apex a blunt point; apotypic, truncate (Figs. 2, 3, and 18B).

09. Ovipositor, stylomere 2, length of nematoid setae.—Four states: plesiotypic, length normal, about 10–50 per cent of length of stylomere 2 (*cf.* Ball and Hilchie, 1983: 100, figs. 2A–C); three apotypic states—a, hypertrophied, as long or longer than stylomere 2 (Figs. 21A–C); b, reduced, about 5 per cent of length of stylomere 2 (*loc. cit.*, 142, fig. 10B); c., absent.

10. Abdominal tergum VIII, extent of sclerotization of dorsal surface.—Four states: plesiotypic, sclerotization continuous medially at anterior margin, desclerotized more posteriorly in a narrow longitudinal or transverse band (Fig. 24); three apotypic states—a, hypertrophied, tergum VIII completely sclerotized medially (Fig. 7); b, medial desclerotized area more extensive, though lateral sclerotized areas with extensive medial projection (Fig. 25); c, medial desclerotized area still more extensive, sclerotized areas reduced to narrow lateral strips (Fig. 26).

The pattern for this character parallels that of sternum X, in that re-sclerotization seems to have taken place in celaenephine adults.

11. Anterior coxal cavities.—Two states: plesiotypic, uniperforate; apotypic, biperforate. The derived character state has been regarded as diagnostic of lebiines by most authors who have written about carabid classification (see, for example, Ball and Hilchie, 1983: 108). Thus, it was something of a surprise to find that adults of the supposedly lebiine genus *Celaenephes* are characterized by uniperforate cavities. It was even more surprising to find both uniperforate and biperforate anterior coxal cavities among the genera of *Cymindina* (coxal cavities biperforate in *Trichis* Klug and *Hystrichopus* Boheman; uniperforate in *Cymindis* [subgenera *Pinacodera* Schaum and *Cymindis sensu stricto*]). Withough a thorough examination of the distribution of states of this character among lebiines, it is impossible to determine unequivocally how to classify the former. Because of the many plesiotypic states exhibited by *Celaenephes* adults, it seems reasonable to hypothesize that the uniperforate cavities of its adults were inherited from the common ancestor of the lebiines, whereas for the subgenera of *Cymindis* (moderately highly derived taxa within a moderately highly derived subtribe) the coxal cavities have probably become uniperforate secondarily, the result of an evolutionary reversal. In fact, however, the uniperforate condition is listed in Table 1 as only plesiotypic.

12. Relative size of right paramere.—Two states: plesiotypic, right paramere about as long as left (see Habu, 1967: 252, fig. 489); apotypic, right paramere much smaller than left, adnate or not to basal part of median lobe.

13. Male genitalia, median lobe, sclerotization of dorsal surface.—Two states: plesiotypic, dorsum almost completely membranous (Figs. 5A and 6A); apotypic, much of dorsal surface sclerotized, membranous portion near preapical orifice, only.

14. Elytron, umbilical series, penultimate puncture.—Two states: plesiotypic, in line with adjacent punctures (Fig. 18B); apotypic, displaced laterally (*cf.* Ball and Hilchie, 1983: 119, fig. 27B).

15. Head: suborbital setae.—Two states: plesiotypic, absent; apotypic, present.

16. Ovipositor, stylomere 2, number of dorsal ensiform setae.—Three states: plesiotypic, two (or more) (Fig. 21B); two apotypic states—a, one; b, zero.

17. Ovipositor, form of stylomere 2.—Two states: plesiotypic, more or less falcate, dorsal margin curved (Fig. 21B); apotypic, not falcate (*cf.* Ball and Hilchie, 1983: 188, figs. 121A, 122A, 123A).

18. Left mandible, premolar tooth.—Two states: plesiotypic, tooth present; apotypic, tooth absent.

DISTRIBUTION OF CHARACTER STATES

Basilewsky (1984: 528) stated that *Celaenephes* is a platynine. Although his conclusion is based on symplesiotypy (characters 12, 13, 16, and 17) and is thus not valid in a phylogenetic system, we concede that the evidence for including *Celaenephes* in the Lebiini based on synapotypy (characters 01 and 02) is not very strong. (Added to the synapotypic features, we note the mid-tibial notches and sensory antennal pits of *Celaenephes*, which, being convergent with some lebiines, might be taken as slight evidence of an underlying similar genetic potential, and hence relationship). Furthermore, the Platynini, as generally diagnosed in terms of adult features, seems to lack synapotypic character states, and so might be a paraphyletic assemblage, one line of which might be the sister group of the Lebiini. Be that as it may, acquisition of the full complement of apotypic features of the Lebiini was likely additive, with new states developing and being incorporated one by one. Thus, a platynine lineage with the features of *Celaenephes* could very well have been the founder stock of the Lebiini, and we believe that this is so. Consequently, we regard *Celaenephes* as a lebiine, without denying its platynine affinities.

The distribution of apotypic character states (Table 1) shows that *Celaenephes* is markedly different from the groups of lebiines with which it has been associated. The characters with apotypic states in *Celaenephes* are over-represented in this study, however, simply because attention is focused on this group. Nonetheless, *Celaenephes* is basically a primitive lineage as shown by the states of characters 11–18. The long secretory groove of the mandibles is also interpreted as plesiotypic within lebiines, though it is apotypic compared to platynines. All features considered, Habu (1982) was well justified in deciding to place *Celaenephes* in a subtribe remote from the Dromiina, and removed from other lebiine subtribes as well.

RELATIONSHIPS OF THE CELAENEPHINA

To establish fully our conclusion that the subtribe Celaenephina exhibits a predominantly plesiotypic combination of character states within its tribe, it might seem necessary to undertake a phylogenetic analysis of the tribe Lebiini. We cannot do so now, though we can offer reference to some published evidence which we think offers adequate support for our conclusion. The single best source is Basilewsky's (1984) remarkable paper that provides figures of the stylomeres for all the groups with which he was familiar (and this includes almost all of the known lebiine stocks), plus reference to other character systems; nonetheless, we do not endorse fully his classification nor his basically typological methods for establishing it. His presentation shows that all of the lebiine groups not referred to in

Table 1. Selected characters and phylogenetic classification and distribution of their states among Platynini and selected subtribes of Lebiini.

Characters		Taxa and Character States ¹				
		Lebiini				
		Platyn.	Celaen.	Perical.	Cymind	Dromina
No.	Designation					
18	L. Mand: premolar tooth	o	o	o	a ⁻	o
17	♀ Stylomere 2: form	o	o	o	a ⁻	a ⁻⁻
16	♀ S2: No. dors. ens. setae	o	o	o	a ⁻	a ⁻⁻
15	Head: suborbital setae	o	o	a	o	o
14	El: umbil. set. punct.	o	o	a	o	o
13	♂ Med. lobe: scl. dors. surf.	o	o	a	a	a
12	♂ Parameres: relative size	o	o	a ⁻	a ⁻	a ⁻
11	Ant. Coxal Cavities	o	o	a	a,o ²	a
10	Tergum VIII: sclerotization	o	a ⁺	a ⁻	a ⁻	a ⁻
09	♀ S2: length nematoid setae	o	a ⁺	o	a ⁻	a ⁻
08	Elytra: form of apex	o	a	o	a	a
07	El: apical marg. microsetae	o	a	o	o,a ³	o
06	L. Mand: terebral tooth	o	a ⁻⁻	o	a ⁻⁻	o
05	Sternum X: sclerotization	o	a	o	o	o
04	L. Mand: ant. ret. tooth	o	a	o	o	o
03	Ant. 4-11: sensory pits	o	a	o	o	o
02	Mandibles: secretory groove	o	a	a	a ⁻	a ⁻
01	Tergum VIII: form lat. margin	o	a	a	a	a

¹ Designation of character states: o plesiotypic; a apotypic; a⁺ apotypic, hypertrophy; a⁻ apotypic, reduction; a⁻⁻ apotypic, loss.

² Genus *Cymindis*, only.

³ Subgenus *Cymindis*, only.

detail above, are structurally more highly derived than the celaenephines, and that none of the former exhibit combinations of character states that would serve to link them closely to the Celaenephina.

EVOLUTION OF STRUCTURAL FEATURES

Although *Celaenephes* may represent an early lineage of Lebiini, adults have acquired some striking features. Perhaps most interesting is the series of sensory pits on the antennomeres. Possible antecedents for such have not been observed in the Lebiini, though the same sorts of structures are characteristic of adults of *Euproctinus* (Shpeley, manuscript in preparation), and *Parena* (tentatively, subtribe *Metallicina*).

A feature that has evolved within *Celaenephes* rather than in the ancestral stock of the genus is the notched middle tibia (Fig. 19), which is characteristic of males of *C. parallelus*. Such tibiae are also characteristic of males of several other lebiine groups, none of which seem to be closely related to one another. Ball and Shpeley (1983: 800) suggested that these tibial notches might be fitted to the edges of female elytra during copulation, thereby improving the ability of a male to cling to the female with which it is mating. Whatever their function, these notches have evolved a number of times in the course of lebiine phylogeny.

The mandibles, though retaining a basically primitive number of teeth and arrangement of ridges, have become distinctive by development of one extra projection on the left mandible, designated as the anterior retinacular tooth. The

terebial tooth, on the other hand, has been lost, a feature shared with cymindines and many other lebiine genera. On the ventral surface of each mandible is a secretory groove in which pores are located. From the latter, filaments project, which appear to be secretions. Such grooves occur on the mandibles of other groups of carabids, such as the Harpalini and Oodini. Evidently, this character has evolved independently in each of the taxa in which it occurs.

The maxillae are remarkable in development of setae on galeomere 2. This seems to be an autapotypic feature of *Celaenephes*. The ligula has also become specialized, with development of the broad and broadly adnate paraglossae.

Taken together, these features indicate rather markedly modified mouthparts. Since this structural complex is involved in obtaining and ingesting food, it seems reasonable to infer that adults of *Celaenephes* either have evolved a markedly distinctive diet, or have a distinctive manner of obtaining and manipulating particles of food.

Additional sclerotization characterizes the posterior part of the body (tergum VIII and sternum X). This seems to be a reversal of a trend in lebiines to reduce sclerotization. Significance of this reversal is not understood.

The stylomeres of the ovipositor, which retain a basically plesiotypic form, have evolved very long nematoid setae. These may be involved with a distinctive mode or place of oviposition, though we cannot offer more detailed suggestions about this topic. The reproductive tract (Fig. 11) is also peculiar, with its very short *bursa copulatrix* and markedly enlarged spermatheca. These structural features are suggestive of a distinctive mode of sperm transfer or storage, but details are not known.

At a more general level, Table 1 shows that of 18 characters studied in detail, most of the derived states involve reduction or loss. Within lebiines, such changes have occurred many times. We suggest, in fact, that evolution of this tribe has been concerned principally with changes in food, feeding, elaboration of defensive mechanisms, and oviposition. (Development of an arboreal way of life is another major trend, but we need not address it because the features considered in this study seem not to be correlated with life above the ground.) We believe that most of the losses and reductions are manifestations of changed, rather than lost, functions. (See, for example, Ball and Hilchie [1983: 110–111] for comments about evolution of the ovipositor.) Consequently, we think that such manifestations are as valuable as obvious structural evolutionary gains, and are thus of substantial use in working out phylogenetic relationships.

CELAENEPHES AND CYMINDIS (SENSU STRICTO)

An alternative view of the relationships of *Celaenephes* favored by one of us (R.B.M.), is that this genus is a highly aberrant derivative of *Cymindis*. This situation has probably been caused by some unusual, and as yet unknown, habits.

The sensory pits of the antennae, the long nematoid seta, and the extra ensiform setae on the second stylomere, the abundant setae on the first stylomere, and the covering of short bristles on the 10th abdominal sternum are very specialized, particularly in regard to oviposition. The changes in the female genitalia could have been reflected in the male median lobe by desclerotization. They may also account for the unusually large differences in the shape of the apex of the median lobe of the two species. Secondary fusion of the hemitergites of the eighth ab-

dominal tergum could be part of the same process. Changes in structure of the mandibles and maxillae are also seen as an adaptation to a different way of life. Both the mouthparts and the genitalia are regarded as being highly responsive to changing circumstances, and thus of limited value in classification.

In general structure *Celaenephes* seems to be markedly similar to *Cymindis* (*sensu stricto*), as illustrated by the following features: brown color, pronotal shape, uniperforate front coxal cavities, pubescent elytra, and simple tarsomere 4. The simple tarsal claws are not far removed from the slightly serrate claws of *Cymindis*. Especially interesting is the rounded, non-sinuate elytral apex of *Celaenephes* and some *Cymindis*, and the apical fringe of microsetae, which in the Lebiini, apparently only these two groups possess.

CONCLUDING STATEMENT

We believe that the data presented demonstrate that the genus *Celaenephes* includes two species, rather than a single one. The combination of character states of *Celaenephes* shows that this taxon probably cannot be included with those lebiine subtribes with which it was associated by authors prior to Habu (1982). So, some of the dark clouds enshrouding the genus seem to have been dispersed. However, a new series of questions has emerged, another layer of cloud, involving environmental partitioning by the closely related species of the genus, and the functional correlates of the remarkable structural features of the adults. The immature stages remain unknown, and their character states will no doubt be of value in testing the hypotheses of relationships proposed here. If *Celaenephes* represents the earliest-evolved extant stock of lebiines, further study of the group ought to provide evidence about the nature of the first stages of the lebiine radiation, and clues about the still earlier ancestral stock of this strikingly diverse tribe of carabids. Because of the potential phylogenetic importance of *Celaenephes*, further study along the lines indicated above ought to prove very rewarding. We hope that some resident of the vast area encompassed by the range of this genus will extend this study.

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LITERATURE CITED

- Allen, R. T. and G. E. Ball. 1980. Synopsis of Mexican taxa of the *Loxandrus* series (Coleoptera: Carabidae: Pterostichini). Trans. Am. Entomol. Soc. 105: 481-576.
- Andrewes, H. E. 1919. On the types of Oriental Carabidae in the British Museum, and in the Hope Department of the Oxford University Museum. Trans. R. Entomol. Soc. Lond. Pp. 119-217.
- . 1923. On the types of Carabidae described by Schmidt-Goebel in his *Faunula Coleopterorum Birmaniae*. Trans. R. Entomol. Soc. Lond. Pp. 1-63.
- . 1927a. Papers on Oriental Carabidae—XX. Ann. Mag. Nat. Hist. Series 9, 20: 263-272.
- . 1927b. Carabidae, in *Insects of Samoa*, Part IV. Coleoptera. Pp. 1-14.
- . 1929. Fauna Sumatrensis. (Beitrag Nr. 64). Carabidae (Col.). Tijdschr. Entomol. 72: 303-340.
- . 1930a. Catalogue of Indian Insects. Part 18—Carabidae. Government of India. Pp. 1-389.
- . 1930b. Fauna Buruana, Coleoptera, Fam. Carabidae. Treubia 7, suppl.: 331-347.
- . 1947. Entomological results from the Swedish expedition 1934 to Burma and British India. Ark. Zool. 38A (20): 1-49, plates I-VI.
- Ball, G. E. 1975. Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). Quaest. Entomol. 11: 143-242.
- Ball, G. E. and G. J. Hilchie. 1983. Cymindine Lebiini of authors: redefinition and reclassification of genera (Coleoptera: Carabidae). Quaest. Entomol. 19: 93-216.
- Ball, G. E. and D. Shpeley. 1983. The species of eucheiloid Pericalina: classification and evolutionary considerations (Coleoptera: Carabidae: Lebiini). Can. Entomol. 115: 743-806.
- Basilewsky, P. 1984. Essai d'une classification supragénérique naturelle des Carabides Lébiens d'Afrique et de Madagascar. (Coleoptera Carabidae Lebiinae). Rev. Zool. Afr. 98(3): 525-559.
- Bates, H. W. 1886. On the Geodephagous Coleoptera collected by Mr. George Lewis in Ceylon. Ann. Mag. Nat. Hist. Series 5, 17: 68-81, 143-156, 199-212.
- . 1892. Viaggio di Leonardo Fea in Birmania e regioni vicine. LXIV. List of the Carabidae. Ann. Mus. Civ. Stor. Nat. Genova Serie 2 12: 340-428.
- Blackburn, T. 1894. Notes on Australian Coleoptera with descriptions of new species. Part XV. Proc. Linn. Soc. N. S. W. Series 2, 9: 85.
- Bouchard, J. 1903. Insectes recueillis par M. le professeur Dr Förster à Bornéo, Java et Sumatra (Palemang) Coléoptères Carabiques. Ann. Soc. Entomol. Fr. 72: 169-176.
- Csiki, E. 1915. Carabidae von den Samoainseln. Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch Naturwissenschaftliche Klasse. Wien 91: 164.
- . 1932. Carabidae: Harpalinae VII, pars 124. Pp. 1279-1598 (Vol. III). In W. Junk and S. Schenkling (1909-1940), *Coleopterorum Catalogus*, 170 parts, 30 vols. Berlin and 's-Gravenhage.
- Darlington, P. J., Jr. 1968. The carabid beetles of New Guinea Part III. Harpalinae (continued): Perigonini to Pseudomorphini. Bull. Mus. Comp. Zool. 137(1): 1-253.
- . 1970. Coleoptera: Carabidae including Cicindelinae. Insects of Micronesia 15(1): 1-49.
- Erwin, T. L. 1974. Studies on the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: a revision of the New World—Australian genus *Pericompsus* LeConte. Smithson. Contrib. Zool., No. 12, Washington, D.C. iv + 96 pp.
- Habu, A. 1960. Notes and descriptions of the Carabidae from Mt. Hiko and its vicinity (Coleoptera). Esakia 2: 3-6.
- . 1967. Fauna Japonica. Carabidae Truncatipennnes Group (Insecta: Coleoptera). Biogeographical Society of Japan, Tokyo Electrical Engineering College Press. Pp. 1-338, 27 plates.

- . 1982. Revised and supplementary notes on and descriptions of the Truncatipennes group of Japan (I). (Coleoptera, Carabidae). Entomol. Rev. Japan 36(2): 85–142.
- Jedlička, A. 1963. Monographie der Truncatipennen aus Ostasien. Lebiinae—Odacanthinae—Brachyninae (Coleoptera, Carabidae). Entomologische Abhandlungen und Berichte aus den staatlichen Museum für Tierkunde in Dresden, pp. 269–579, plates.
- Lacordaire, J. T. 1854. Histoire Naturelle des Insectes. Genera des coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes, vol. 1. Paris 486 pp., illus.
- Landin, B.-O. 1955. Entomological results from the Swedish expedition 1934 to Burma and British India. Coleoptera: Carabidae collected by René Malaise. Ark. Zool. (N.S.) 8: 399–472, plates I–III.
- Liebherr, J. K. 1983. A cladistic analysis of *Agonum* and allied genera, with a systematic revision of the *A. extensicolle* species group (Coleoptera: Carabidae). Ph.D. Dissertation, Department of Entomology, The University of California, Berkeley.
- Schmidt-Göbel, H. M. 1846. Faunula Coleopterorum Birmaniae, adjectis nonnullis Bengaliae indigenis. Lieferung 1. Prag. viii + 94 pp., plates 1–3.
- Walker, F. 1858. Characters of some apparently undescribed Ceylon insects. Ann. Mag. Nat. Hist. Series 3, 2: 202–209, 280–286 [continued in Volume 3].
- Watrous, L. E. and Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Systematic Zoology 30(1): 1–11.
- Wiley, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley and Sons, New York, Chichester, Brisbane, Toronto xvi + 439 pp.